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FUSION OF CERVICAL VERTEBRAE IN THE ERETHIZONTIDAE AND DINOMYIDAE

BY CLAYTON E. RAY

Comparative postcranial osteology has been a curiously neglected source of evidence in the study of relationships among caviomorph and hystricomorph rodents though Landry, 1957, pp. 5-30, has made some use of postcranial osteology on the subordinal level. It seems useful, therefore, to call attention to a peculiarity observed in the cervical vertebrae of the living erethizontine (Fig. 1) and dinomyid (Fig. 2) caviomorphs. The second (axis) and third cervicals are firmly fused together in *Erethizon*, *Coendou*, *Echinoprocta* (the postcranial skeleton of *Chaetomys* is apparently unknown), and *Dinomys*. This condition was noted by Giebel (1877, p. 273) for *Coendou* (=*Cercolabes*) only and has apparently not been recorded in the literature since, having been overlooked, for example, by Scott (1905, p. 422) in contrasting the skeletons of *Sciamys* and *Erethizon*, by Anthony (1926, pp. 124, 126) in his detailed comparison of the skeletons of *Elasmodontomys*, *Erethizon*, and *Dinomys*, and by Swena and Ashley in their recent (1956, pp. 8-10) osteology of *Erethizon*. The first four cervicals are missing from the type (in part) skeleton of *Dinomys* figured by Peters (1873, Pl. 3, fig. 4). Landry (1957, p. 46) and Fields (1957, pp. 337, 341, 384) have mentioned but not described the tendency toward fusion of cervical vertebrae in *Dinomys* and in *Olenopsis*.[1]

Cervical vertebrae of the following caviomorph and hystricomorph genera have been available for examination or are ade-

[1] Patterson (personal communication) questions Fields' (1957, p. 323) assignment of his Colombian material to the genus *Olenopsis*. Thus, even though the animal described is a dinomyid, it is not necessarily true that *Olenopsis* is a dinomyid.

quately described in the literature: *Acanthion, Thecurus, Hystrix, Atherurus, Trichys, Erethizon, Coendou, Echinoprocta, Eocardia* (Scott, 1905, p. 465), *Schistomys* (Scott, 1905, p. 482), *Cavia, Kerodon, Galea, Prodolichotis* (Fields, 1957, p. 373), *Dolichotis, Hydrochoerus, Dinomys, "Olenopsis"* (the material from the La Venta of Colombia, not the Santa Cruz of Patagonia), *Elasmodontomys, Amblyrhiza, Cuniculus, Dasyprocta, Myoprocta, Perimys* (Scott, 1905, p. 437), *Lagostomus, Lagidium, Chinchilla, Neoreomys* (Scott, 1905, p. 395), *Capromys, Geocapromys, Plagiodontia, Myocastor, Sciamys* (Scott, 1905, p. 422), *Ctenomys, Abrocoma, Isolobodon, Proëchimys, Hoplomys, Isothrix, Echimys, Dactylomys, Thryonomys,* and *Bathyergus.* Included in this list is at least one representative from every family of caviomorph and hystricomorph rodents (as given by Wood, 1955) excepting the Petromuridae. It is not likely that the condition of the cervicals in this monotypic African family would alter the general picture in any way. In none of the genera listed, save the three erethizontids and *Dinomys*, was cervical fusion noted.

ERETHIZONTINAE

The fusion in *Erethizon* is typical of the Erethizontinae and will serve as the basis for description. Some two dozen individuals were examined. The neural spine of the third cervical is here relatively higher than in mammals generally and is enveloped on either side by the broad lateral lamellae of the neural spine of the axis. The two neural spines become more broadly fused to one another with increasing age (though in part distinguishable in all specimens seen). In immature individuals the lateral lamellae of the axis are closely applied to the neural spine of the third cervical but are not fused to it, and in one individual (MCZ[2] 811) diverge posterodorsally to form a bifid process. The area of most profound fusion is between the postzygapophyses of the axis and the prezygapophyses of the third cervical, the trace of the articular surface becoming obliterated with age. Although the centra become tightly fused, particularly near the ventral midline, their

[2] Throughout the discussion MCZ refers to Museum of Comparative Zoology, AMNH to American Museum of Natural History, CNHM to Chicago Natural History Museum, and UCMP to University of California Museum of Paleontology.

union is in part discernible in all individuals. The pleurapophyses of the axis approach those of the third cervical quite closely, but attain contact in only one individual (MCZ 819), in which the distal extremity of the right pleurapophysis (only) of the axis touches and is narrowly fused to the dorsolateral surface of the corresponding pleurapophysis of the third cervical. In none of the specimens examined was there any suggestion of fusion between the third and fourth cervicals.

DINOMYIDAE

Dinomys is represented by two subadult skeletons[3] (CNHM 66891 and 57186), by a young adult skeleton (CNHM 69593), and by an adult skeleton in part pathological (AMNH 70354). The nature of the fusion between the axis and third cervical is very similar to that in the Erethizontinae. Already in the immature individuals the neural spines are closely appressed and largely fused, whereas the mutual zygapophyseal articulations are completely and indistinguishably fused. As in some individuals of *Erethizon*, the lateral lamellae of the axial neural spine in all four specimens of *Dinomys* diverge posterodorsally to form a bifid process. These lamellae are broadly separated in CNHM 69593, and the intervening space is occupied by the neural spine of cervical three and by a connecting network of cancellous bone. In CNHM 57186 (Fig. 2A) and in AMNH 70354 a slit-like foramen situated on either side just medial to the zygapophyses passes into the neural canal between the neural arches of the axis and third cervical. This foramen may be interpreted as the vestige (preserved here for the passage of nerves and blood vessels) of the open space normally present between the neural arches of successive vertebrae. It is not present in CNHM 66891, and is but inconsistently and weakly developed in the erethizontids examined. There is on the articular facet of each postzygapophysis in CNHM 69593 a small foramen with a well-defined channel extending from it to the posterior (right) and postero-

[3] Not adults as stated by Fields (1957, p. 320), but subadults judging from the slight wear undergone by $P\frac{4}{4}$, the open basisphenoid-basioccipital sutures, and the open epiphyses throughout the skeleton. The young adult is characterized by $P\frac{4}{4}$ in full use, closed basisphenoid-basioccipital suture, open vertebral epiphyses, and tight but discernible limb epiphyses.

medial (left) edge of the facet. I suspect that this foramen is homologous to the one discussed above, and that the functionally single postzygapophysis is in fact compounded from a posterolateral contribution from the axial postzygapophysis and an anteromedial contribution from the third cervical postzygapophysis. This suspicion is reinforced by the presence of complementary subdivisions in the prezygapophysis of cervical four (particularly the left), by the enveloping of the third cervical by the axis to a greater extent than in any other specimen of *Dinomys*, by the juxtaposition of the supposed axial postzygapophyses and the lamellae of the axial neural arch, and by the complete absence of the line of fusion as seen in lateral view in the other *Dinomys* specimens examined (Fig. 2A). Although the vertebral epiphyses (and second intercentrum at the base of the odontoid process) remain open throughout the column in the subadult and young adult specimens, the epiphyses between axis and third cervical are fused together (Fig. 2B). As in the erethizontines the pleurapophyses on either side approach closely but do not touch except in the youngest individual (CNHM 66891) in which the distal extremity of the left axial pleurapophysis is fused narrowly to the dorsal surface of the pleurapophysis of the third cervical. The pleurapophyses of the axis in CNHM 69593 are peculiarly developed into broad lamellae which extend posterodorsally lateral to the prezygapophyses of cervical four. Neither in the two subadult individuals nor in the young adult are cervicals three and four fused to one another. However, in the older of the two subadults (CNHM 57186) and in the young adult (CNHM 69593), roughened areas are present immediately anterior to the postzygapophyses of cervical three, posterior to the prezygapophyses of cervical four, and in the area of contact between the neural spines, suggesting the possibility of fusion at these points, with increased age. The contact surface between centra three and four in CNHM 69593 is not at all planar but curves anteriorly at both dorsolateral corners. Clearly very little movement could have occurred between cervicals three and four in this individual. AMNH 70354 presents a special problem owing to its pathological nature and to the lack of a series of normal adult skeletons from which to determine the average condition. Here the centra of cervicals two through seven are fused as are

the neural spines and zygapophyses of cervicals two through five. The fusion of the centra between cervicals five and six and between six and seven is effected by gross ventral exostoses. Otherwise cervicals five through seven are independent of one another just as they are in the three younger individuals at hand and in the subadult figured by Peters (1873, Pl. 3, fig. 4), all of which strongly suggests that these vertebrae are not ordinarily fused in *Dinomys.* The fusion of centra two through five may be enhanced by lesser exostoses. All post-atlantal cervicals are more or less marked by the rugose, spongy, asymmetrical growth indicative of pathology, as are many of the other vertebrae (notably the posterior thoracic and anterior lumbar). However, the exostoses are not so pronounced as to definitely indicate that cervicals four and five are here abnormally included in the fused series. That cervical five was not fused to cervical four in the type skeleton is clearly shown by the accidental loss of the fourth and the preservation of the fifth (Peters, 1873, p. 231). On the basis of the condition in the subadult and young adult animals (and its analogy to the erethizontines) and the pathology of AMNH 70354, it seems reasonable to conclude tentatively that only cervicals two and three are normally fused in *Dinomys,* and that cervical four may be added in older animals. The final solution awaits more specimens.

Thus *Dinomys* and the erethizontines are very similar in the fusion of cervical vertebrae, with the reservation that fusion seems to be more variable in nature and extent in *Dinomys* than in the erethizontines (judging from the considerable diversity observed among only four individuals of *Dinomys*). Certain differences may be noted in the morphology of the vertebrae in the two groups. The anterior articular facets of the axis in erethizontines are entirely convex and situated on low pedestals serving to separate them from the peglike odontoid process, whereas in *Dinomys* the facets are concave in frontal section in such a way that they form a curved surface continuous medially with the bluntly conical odontoid process (cf. Figs. 1B, 2B). In the erethizontines the centra of cervicals two and three are relatively deep dorsoventrally, with a prominent anteroposterior mid-ventral ridge (especially in *Erethizon* and *Coendou*); in *Dinomys,* relatively shallow dorsoventrally with a flattened venter. In

Erethizon the articular facets of the postzygapophyses of cervical three are situated relatively high on the neural arch, are about equally laterally and ventrally directed, planar, and somewhat isolated from the body of the neural arch; in *Dinomys* the articular facets are relatively low, dominantly ventrally directed, concave in transverse section, and an integral part of the neural arch (cf. Figs. 1C, 2C).

Of extinct erethizontids and dinomyids only the dinomyid from the La Venta Miocene of Colombia, described by Fields (1957, p. 323, et sqq.) under the name *Olenopsis* (=*Drytomomys*) *aequatorialis* (Anthony) 1922, includes cervical vertebrae. The specimens preserved are both articulated series of subadult vertebrae, the one set (UCMP 39969) including a fragment of the left postzygapophysis of the axis and cervical three through thoracic one, all perfectly preserved excepting the distal extremities of pleurapophyses; the other set (UCMP 41636) including most of the neural arch and spine of the axis, complete (excepting pleurapophyses) cervicals three, four, and five, and fragmentary cervicals six and seven lacking portions of the neural arches. I am very sorry to be unable to agree with Fields' characterization (1957, p. 337) of the cervical vertebrae as "showing tendency toward fusion of anterior part of series, as in *Dinomys*." I can discover no certain evidence for fusion between any of the vertebrae preserved. The prezygapophyses and anterior end of the centrum of cervical three in UCMP 39969 bear well-preserved, smooth articular facets as in normal diarthroses. The fragment of the left postzygapophysis of the axis adhering to the third cervical appears to be merely cemented by matrix as are the articulations in all cases. The anterior articular facet of cervical three is exposed and smooth also in UCMP 41636. The neural arch of the axis in this specimen is slightly skewed upon that of cervical three in a clockwise direction as viewed from above with the result that the two vertebrae are not perfectly articulated but are separated by a thin layer of cementing matrix. The two neural spines are nowhere in contact, that of cervical three being quite low as in the succeeding cervicals and unlike the tall spine of the third cervical in *Dinomys*. That the absence of fusion in the fossils is not due merely to immaturity is shown by the youngest speci-

men of *Dinomys* (CNHM 66891) the dentition of which is comparable in stage of wear to that of the dentigerous elements associated with each of the fossils (Fields, 1957, Figs. 15, 16A, 16B). The possibility remains that fusion could have occurred later in the ontogeny of the extinct form, but even granting this possibility the tendency could have been by no means as strong as in *Dinomys*.

TAXONOMIC DISCUSSION

Evidence from myology (Parsons, 1894, pp. 295-296; Wood and White, 1950, p. 592), external characteristics (Pocock, 1922, p. 422), parasitology (Vanzolini and Guimarães, 1955, p. 43), dentition (Wood, 1950, p. 95), serology (Moody and Doniger, 1956, p. 54), and paleontology and paleogeography (Wood, 1955, p. 180) has clearly indicated that erethizontids and hystricids show no particular resemblances to one another beyond the possession of quills,[4] structures shared also with hedgehogs, echidnas, and some tenrecs as well as with other rodents. This distinctness of New and Old World porcupines was recognized by some workers many years ago (e.g. Tullberg, 1899, p. 108), but only recently has the opinion been expressed that erethizontids are isolated from other caviomorphs. Simpson (1945, p. 94) followed by Wood (1955, p. 182) has accorded superfamilial rank to the New World porcupines, whereas Moody and Doniger (1956, p. 53) have asked, "Should the erethizontids be accorded their own suborder?" In support of this suggested isolation are the findings that *Erethizon* is serologically as distinct from *Cavia* and *Dasyprocta* as from *Hystrix* (Moody and Doniger, 1956, p. 52), that erethizontid Mallophaga fall into one isolated group and those of other caviomorphs into another (Vanzolini and Guimarães, 1955, pp. 30, 31), and that "Deseadan caviomorphs are all very closely related, except for the erethizontids, which were already distinct" (Wood, 1955, p. 182). It should be

[4] In point of fact, the quills are structurally rather dissimilar in the two groups. For example, the distal portion of the quill in all three genera of Erethizontinae is furnished with a covering of imbricate, proximally directed barbs (described and illustrated for *Erethizon* by Loweg, 1900, p. 853, Pl. 28, fig. 6 and by Shadle and Po-Chedley, 1949, p. 173, fig. 1), whereas I am able to find such barbs in none of the five genera of Hystricidae (Loweg, 1900, p. 853 notes their absence in *Hystrix cristata* and none are described by Lochte, 1957 in his detailed study of the quills in *Hystrix hirsutirostris*).

pointed out that the serological, parasitological, and (Deseadan) paleontological information is unknown for dinomyids, which therefore cannot on these grounds be summarily lumped with "other caviomorphs" as opposed to erethizontids. Aside from the similarity in cervical fusion demonstrated here, Pocock (1926, p. 228) has noted a "tolerably close resemblance" between the feet of *Dinomys* and of *Erethizon* and *Coendou,* and Fields (1957, p. 348) has pointed out the similarity of the auditory ossicles in *Erethizon, Dinomys,* and *Olenopsis aequatorialis.* Attractive as this evidence is, it furnishes an inadequate basis for asserting any special relationship between erethizontids and dinomyids. Indeed contrary evidence from dentition and cranial osteology seems at present to be more compelling. In this connection the relationship between the axis and third cervical in *Chaetomys* and in the Deseadan erethizontids will, when known, be of great interest in helping to determine, respectively, the affinities of *Chaetomys,* and the antiquity of fusion in the erethizontids. If fusion had already taken place in the Deseadan (Oligocene) erethizontids then it might reasonably be concluded that the fusion in dinomyids is independent since it apparently had not occurred by late Miocene time. Furthermore, one would expect fusion to occur in *Chaetomys* if it is truly an erethizontid.[5]

In conclusion, present evidence indicates that the constant and exclusive fusion of cervical vertebrae two and three, together with the morphological features described above, furnishes a valid taxonomic character for the living Erethizontinae. Appraisal of the possible broader value of the character awaits evidence from *Chaetomys,* normal adult *Dinomys,* and fossil erethizontids (and additional fossil dinomyids).

[5] A cautionary, if confusing, example is provided by the Pedetidae, in which cervical fusion may prove to be irregularly distributed. Hatt (1932, pp. 640, 715) found cervicals two and three to be fused in *Pedetes surdaster* but not in *P. cafer* (as Hatt was well aware, this character should be checked on more specimens than were available to him). In early Miocene time fusion had not taken place in *Megapedetes* (MacInnes, 1957, p. 13) but may well have taken place in the more specialized *Parapedetes.* Stromer (1926, pp. 130, 131) does not mention fusion in his description of the cervical vertebrae of *Parapedetes,* but the specimen was embedded in matrix and the character could easily have been overlooked. It goes almost without saying that the pedetids are so remote from caviomorphs and the fusion of their cervical vertebrae is a response to such different selective pressures that this common character is of no taxonomic significance whatever.

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